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Author(s): R. Gerald Wright and George M. Van Dyne
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# POPULATION AGE STRUCTURE AND ITS RELATIONSHIP TO THE MAINTENANCE OF A SEMIDESERT GRASSLAND UNDERGOING INVASION BY MESQUITE

R. GERALD WRIGHT AND GEORGE M. VAN DYNE

ABSTRACT.—Data from long-term chart quadrats recorded from the Jornada Experimental Range in south-central New Mexico were used to develop demographic measurements for black grama and mesa dropseed. These measurements included mean and maximum lifespans, survival probabilities, and rates of establishment and were used to derive the stable age structure for black grama. They were combined with factors such as climate and grazing in a model designed to simulate the long-term dynamics of a stable perennial grassland. Using the stable age structure as a starting point, the model was perturbed by differentially lowering the age-specific survival rates in an effort to mimic the effect of mesquite competition. A stable age structure for black grama was achieved after a period of 40 years. A similar structure for mesa dropseed could not be derived. Output of the model run over a 47-year period in the absence of mesquite shows that stability of numbers in each class can be achieved over the entire time period. Grazing does not appear to disrupt this stability, but only decreases the number of plants established each year. Simulation of increased mesquite competition showed that in the first 12 years there may be a concomitant decline in the number of new individuals. By the 25th year, the survival rates for all but the oldest individuals have been adversely affected and there are few individuals alive.

Demographic data on vegetation communities adequate to assess the changes that these communities have undergone in response to past environments is rare for herbaceous plants (Harper and White, 1974). This is because the precise ages for such plants are seldom determinable. Continuous data spanning long time periods provide an alternative method to study plant population age structure and survivorship.

There is one large set of historical data that has been collected over a long-term period on semidesert grasslands (Paulsen and Ares, 1962; Buffington and Herbel, 1965). These data come from the systematic recording of permanently established quadrats, which, when charted over a period of years, produce a large number of maps, each illustrating the basal areas of individual plants. Usually, these data are lumped to give only percentage cover for a given year (Nelson, 1934). When the records of the individual plants are considered, extremely large amounts of data, including mean and maximum lifespans and survival rates, are obtained, thus yielding demographic parameters as discussed by Wright (1972) and Wright and Van Dyne (1976).

An important management concern has been the dramatic spread of mesquite (*Prosopis juliflora*) on these grasslands. In less than 50 years it has come to occupy about 58% of a once predominant perennial grassland community (Buffington and Herbel, 1965). In sandy windswept areas, the many-stemmed mesquite plant traps blowing soil, creating dunes and eventually eliminating most of the soil and grass cover between the plants (Branscomb, 1958). As early as 1929, Campbell recognized that the cycle of mesquite spread and dune formation might be self-regenerating. Much research has since been undertaken to develop control measures for mesquite (Scifres and Polk, 1974; Cable and Martin, 1975) but the underlying mechanisms of its spread and success are not clear.

The objectives of this paper are to develop a model of the demographic parameters of a stable perennial grassland community and the factors which influence them such as climate and grazing, and to use this model to study a hypothetical mechanism underlying the successful invasion of mesquite.

EXPERIMENTAL AREA.—Field data were provided by the Agricultural Research Service, USDA, from the Jornada Experimental Range, a 42,775 ha grazing area in southeastern New Mexico (USDA, 1951). The Jornada is a semidesert, grass-shrub complex similar to that which occupies much of the plains area extending over southeastern Arizona, southern New Mexico, western Texas, and northern Mexico (Jardine and Forsling, 1922; Campbell and Campbell, 1938; Martin, 1975).

The chart quadrats used were located in the black grama (*Bouteloua eriopoda*) vegetation type, which is common on the well-drained sandy and gravelly soils of the dry mesas. Associated species include: mesa dropseed (*Sporobolus flexuosus*), red threeawn (*Aristida longiseta*), and poverty threeawn (*Aristida divaricata*). The principle shrub is mesquite.

Records kept since 1915 show an annual precipitation of about 23 cm, of which about 70% occurs between 1 April and 30 September, normally in the form of high-intensity thunderstorms. Additional precipitation data were taken from a network established in 1920 of 20 storage rain gauges distributed over the range. Over a 60-year period, the mean precipitation of 23 cm has a coefficient of variation of 87%.

The soils on the Jornada Plain lack humus and show little textural change between the surface and subsoil (Gile, 1961, 1977). The lime content is high in all soil types and this grades into a calcareous layer at various depths in the coarser soils (Shreve and Mallory, 1933).

Records show that as early as 1860 herds of sheep, cattle, goats, and horses were driven across the Jornada Plain from Chihuahua, Mexico, to Sante Fe. By the turn of the century, overgrazing was generally the case over most of New Mexico's rangelands (Pingrey, 1948; Wooten, 1908). Before 1912, the Jornada and surrounding area was heavily grazed by cattle. Records on the use of the experimental range by cattle have been kept since 1912 on a pasture basis. In 1916, the stocking was at about 17 ha per animal annually whereas, in recent years, there has been about 95 ha per animal unit. A seasonal suitability system (Valentine, 1967) was long used for experimental grazing management on the Jornada. Cattle were removed from the black grama pastures during the summer-fall growing season, and returned to them from October to July (Ares, 1943; Pearse, 1950).

METHODS.—The Jornada quadrats were charted annually from 1915 through 1968 with the exception of a few years from 1954 through 1967. We reread the quadrats in 1968. Data have been used from about 35 quadrats selected out of the 90 that were charted for more than 30 years. Only those quadrats dominated by black grama were selected. The methodology used to convert the quadrat records into a computer-compatible form and to process and analyze them has been described by Wright and Van Dyne (1970, 1976) and Wright (1972*a*, *b*).

*Stable Age Structure*.—A model is always a simplification of real life. We chose to simplify the Jornada ecosystem by focusing attention on the populations of black grama grass, as a long-lived dominant plant, and mesa dropseed grass, as a shorter-lived subdominant plant.

One method of characterizing how well a population is adjusted to environmental demands and changes in conditions is by the stability of its age structure. That is, the point at which the ratio of the numbers of individuals in each age class remain the same from one unit of time to another. A model of the age structure of animal populations was formulated by Leslie (1945, 1948) and described by Williamson (1959) and Usher (1966), and was adopted for this study. Leslie's matrix equation is:

$$Mn_t = n_{t+1} \qquad (1)$$

Where

$$M = \begin{bmatrix} f_0 & f_1 & f_2 & . & . & . & f_{m-1} & f_m \\ P_0 & . & . & . & . & . & . & 0 \\ 0 & P_1 & . & . & . & . & . & 0 \\ 0 & 0 & P_2 & . & . & . & . & 0 \\ . & . & . & . & . & . & . & . \\ . & . & . & . & . & . & . & . \\ 0 & 0 & 0 & . & . & . & P_{m-1} & 0 \end{bmatrix} \quad \text{and} \quad nt = \begin{bmatrix} n_{0,t} \\ n_{1,t} \\ . \\ . \\ . \\ . \\ N_{m,t} \end{bmatrix}$$

Where in this context:

$P_x$ = the probability that a plant of age x survives and will enter the age class x + 1.

$f_x$ = the average number of plants established in a given time period which are attributable to plants of age x.

$n_{x,t}$ = the number of plants of age class x at time t.

*Model Structure.*—Data on establishment, survival, and death of both black grama and mesa dropseed, and the influence of environmental factors on these measures were combined in a compartmental demographic model in an attempt to simulate the long-term population dynamics of these species. The model structure is shown in Fig. 1. We follow the life history of the plants of both species for a given area, from establishment through each of eight yearly age classes. The flows between the compartments, the $P_x$ and $f_x$, are based on multiple regression equations relating survival to present and past climatic conditions. The establishment of new plants, ($f_x$), is treated as a function of the level of grazing, the amount of rainfall, and competition.

The effect of grazing and yearly precipitation on establishment of both species was analyzed by Wright and Van Dyne (1976). Plant establishment was shown to be deterred at higher grazing levels, primarily because of cattle movement and trampling, and was enhanced by above average precipitation during the growing season. In most cases, because of low densities, the detrimental effects of competition were not evident. There was a positive relationship between the number of plants established and the number there the previous year (in effect a source of seeds or rooting sets).

Wright and Van Dyne (1976) also found a strong relationship between rainfall measured as the number of days of effective moisture (sufficient to add to soil moisture) in a given time period and the survival rates between age classes. These conclusions agree with finds by Cable (1975). There was also a corresponding relationship between the rainfall during the year of establishment and the subsequent survival rates of that cohort of plants. The level of grazing appeared to have little affect on plant survival.

The above factors were combined as illustrated in Fig. 1 to calculate the establishment, survival, and mortality flows. Establishment was determined as a function of intraspecific ($X_1$) and interspecific ($X_2$) numbers of plants of various age classes, precipitation ($X_3$), and grazing level ($X_4$).

$$\text{total yearly establishment} = f_x = \{k_1X_4\} \{\max [0, (k_2 + k_3X_1 + k_4 X_1^2 + k_5X_2 + k_6X_3)]\} \qquad (2)$$

where $k_i$ are coefficients determined in regression analyses and $x_i$ are defined above, and $k_1X_4$ takes on a value of 1.00, 1.10, and 1.15 for the different grazing levels, approximating locations of close, medium, and long distances from livestock watering points. The total number of plants established were then allocated equally among all age classes (each $f_x$).

The probability of a plant surviving from one age class to the next (for the first seven age classes) was determined as a function of days of effective moisture ($X_1$), climate in the year of establishment ($X_2$), a random component ($X_3$), and an age-specific factor ($X_4$), as follows:

$$P_x = k_1 + k_2X_1 + k_3X_2 + k_4X_3 + k_5X_4 \qquad (3)$$

where the $k_i$ are determined in regression analyses and are specific for each age and species of plant. Further details and parameter values are given in Wright (1972). The plants dying represent those not surviving to the next age class. We assumed no plants lived past age class eight.

Leslie (1966) points out that the age distribution of any population will continue to remain stable only if the mortality caused by an outside agent is constant among all age classes over all periods of time. Any mortality force that is not constant over all age classes will disrupt the stable age distribution and introduce oscillations. Furthermore, the changes in the population will be

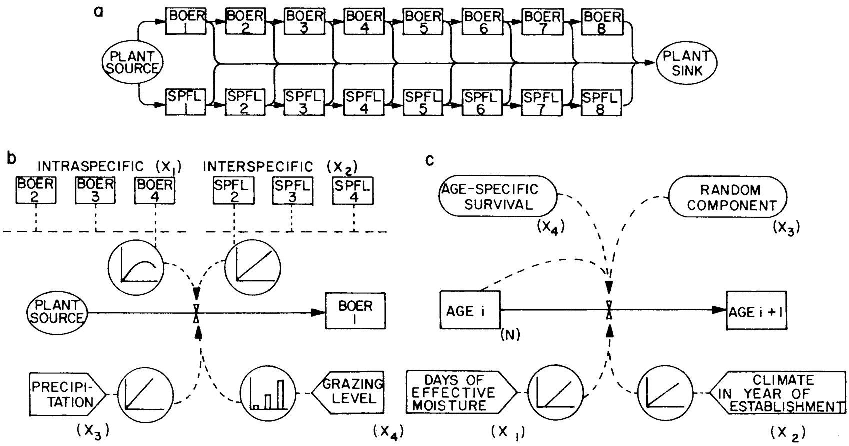

FIG. 1.—A compartmental model (a) for predicting numbers of eight age classes of black grama and mesa dropseed plants in a semidesert grassland. Factors controlling establishment (b) are age-specific plant density influences, climate, and grazing intensity. Factors affecting survival and mortality (c) are age-specific mortality, days of effective rainfall, and climate in the year of establishment.

greatest if there is a differential mortality of the younger plants. This is true irrespective of the number of new plants produced under normal years (Demetrius, 1969).

The inverse relationship between the density of mesquite and perennial grass production and cover has been widely recognized (Martin and Cable, 1974; Streets and Stanley, 1938; Reynolds and Martin, 1968). Mesquite may differentially affect the survival of the various age classes of plants by changing the soil moisture relations. Mesquite's root structure not only allows it to use large volumes of water, but to use it inefficiently (Dwyer and DeGarmo, 1970). McGinnies and Arnold (1939) found that native perennial grasses produced about three times as much dry matter per unit of water as did mesquite.

The usurping of water by mesquite at critical times during the life cycle seems to be a key factor in inhibiting the survival of perennial grasses. Wright and Van Dyne (1976) found that effective rainfall had a greater influence on increasing the survival of black grama plants between 3 and 5 years old than for any other age classes.

Our model tested the assumption that mesquite invasion, implemented by differentially decreasing age-specific survival rates, will produce changes in the black grama and mesa dropseed grass populations similar to those found in the historical record.

RESULTS AND DISCUSSION.—*Age Structure of Black Grama.*—The stable age structure for the black grama community was determined using Equation 1 in an iterative fashion until the age structure stabilized. The proportion of individuals in the respective age classes, $n_{xt}$, is about 55, 20, 10, 6, 5, 3, 2, 2, and 1. This age structure has the strong concave curve, common among reproductively active populations possessing a high juvenile mortality.

Starting from any point, a maximum of 40 years is necessary for the age structure of black grama to stabilize. However, a stable age distribution for all but the older age classes is nearly achieved by 15 years (Table 1). Of interest is that the 40-year period required for stability exceeds the general 25- to 30-year cycle of climatic disruption in the Southwest (Green, 1960).

A stable age structure for mesa dropseed did not appear to exist, probably because of its shorter life span and oscillatory pattern of establishment.

TABLE 1.—*The proportional change in the numbers of plants of black grama in each age class for the three different time intervals listed and the preceding time interval.*

| | Age classes | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Time interval | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| 5 years | 1.14 | 1.53 | 0.81 | 0.84 | 4.50 | 0.68 | 0.88 | 0.89 | 0.67 |
| 15 years | 1.14 | 1.15 | 1.13 | 1.16 | 1.14 | 1.13 | 1.17 | 1.18 | 1.19 |
| 40 years | 1.14 | 1.14 | 1.14 | 1.14 | 1.14 | 1.14 | 1.14 | 1.14 | 1.14 |

*Model Dynamics without Mesquite.*—The model was run for all quadrats categorized according to soil type and grazing pattern. The output discussed below is only for that subset of moderately grazed and nongrazed quadrats located in the deep sandy soil areas of the range. Grazing data from the particular pastures and rainfall from the nearest rain gauge were used as driving variables. The model was developed to run over a 47-year period beginning in 1915; a 1-year time step was used. The number of plants in each age class in a 5-$m^2$ area were initialized according to their proportions in a stable age structure.

Model predictions in Fig. 2 illustrate the yearly changes in the numbers of black grama plants in the first seven age classes on nongrazed and grazed sites respectively. Although the number of plants in any given age class may be highly variable between any 2 years, a long-term pattern of stability appears to exist over the entire time period. Grazing does not appear to disrupt this stability, but only decreases the number of plants established each year.

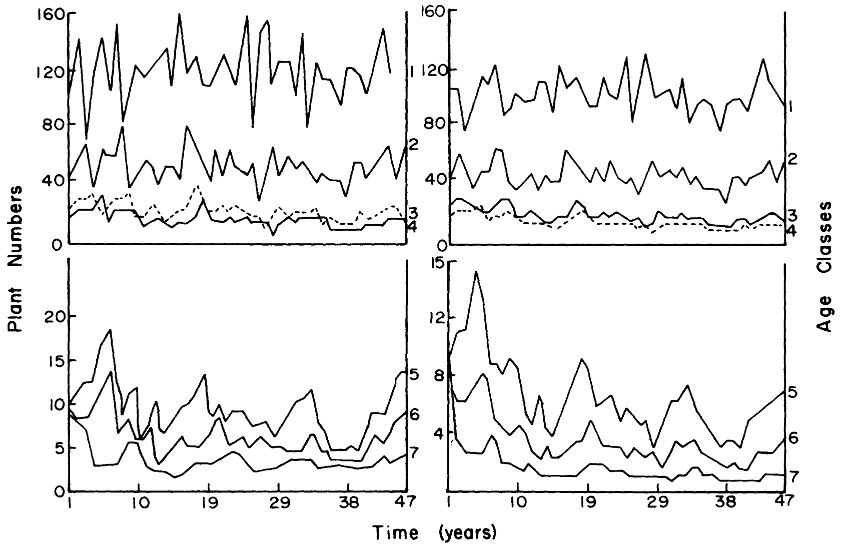

FIG. 2.—Predicted changes in numbers of black grama plants per 5 $m^2$ of seven age classes over 47 years on an ungrazed site (left) and a grazed site (right). Note differences in vertical scales.

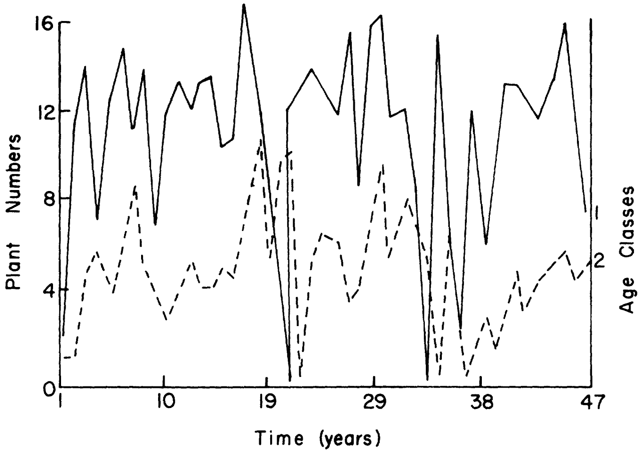

FIG. 3.—Predicted changes in the numbers of mesa dropseed over 47 years for the first two age classes on non-grazed exclosures.

Figure 3 shows the changes in the numbers of mesa dropseed plants on a nongrazed enclosure. Only the first two age classes are depicted due to the lack of survivors in the later age classes. The extreme oscillation between the numbers of plants in corresponding years, particularly in the first age class, appears to be due to the opportunistic establishment characteristics of the species. The numbers established on a grazed site (not shown) are less but the pattern is the same.

The results obtained from the model were compared with the input data upon which the model was based. This was done to measure the extent to which the variation in plant survival is accounted for by the model. It does not imply a validation of the model. Validation of the model with independent data sets has not been done yet, as discussed below. Some results of this comparison are given in Table 2. The variation between that predicted and measured is greatest in the earlier age classes and diminishes as the plants age. However, the model runs were made with a stable age distribution as initial conditions in 1915 rather than the field data. The deviations are positive and are greater for younger than for older age classes.

*Model Dynamics with Mesquite Invasion.*—Commencing with a black grama community with a stable age structure, the model was used to simulate the invasion of mesquite through three stages. The impact of new mesquite in the community was modeled by adjusting the coefficients governing competition for water. The coefficients were arbitrarily increased by 15%. The impact of established mesquite plants was included in the model by

TABLE 2.—*A comparison of results obtained in the model with those data on which the model was based. The figures represent the average deviation between that predicted and the actual data as a percent of the predicted. Data are for black grama on grazed sites (Fig. 2).*

| Age classes | | | | | | | |
|---|---|---|---|---|---|---|---|
| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| 24 | 22 | 16 | 17 | 14 | 12 | 11 | 9 |

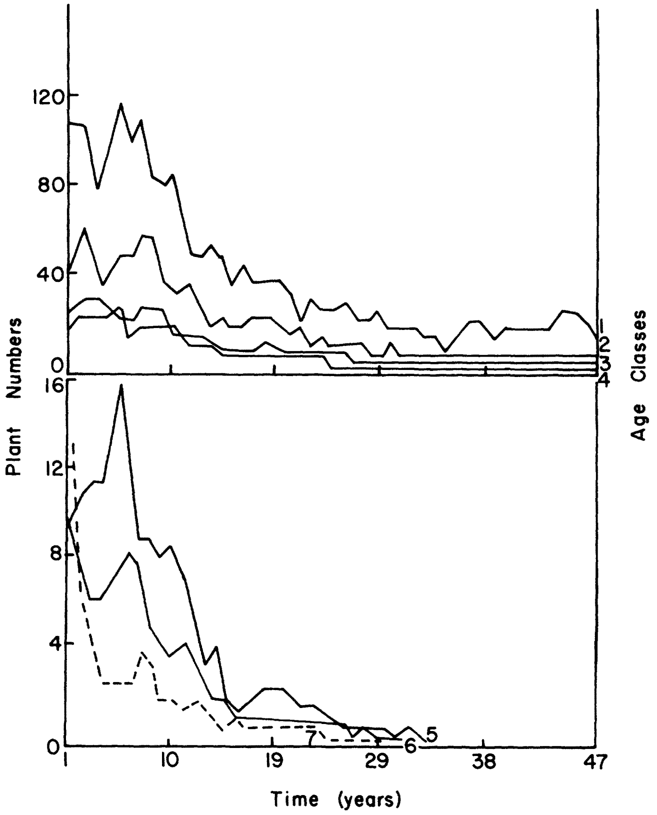

FIG. 4.—Predicted changes in numbers of black grama plants per 5 $m^2$ of seven age classes on grazed quadrats undergoing invasion by mesquite.

assuming age specific survival rates would be decreased due to reduction in available soil water (Cable, 1977). The output of the model is shown in Fig. 4.

In the first 12 years following the establishment of new mesquite plants, there may be concomitant decline in the number of new individual grass plants. This may partially be due to the competition for space and moisture, but also because the thorny mesquite alters cattle travel routes, increasing the trampling and uprooting of fragile young plants. Glendening and Paulsen (1955) have shown how rapidly large numbers of new mesquite plants can become established where conditions are favorable.

The growing mesquite plants with their large lateral root systems are better able to extract the limited soil water than the grasses. While this competition adversely influences plants in all age classes, it is most critical to those plants in age classes three through five. Young plants with shallow root systems can obtain surface soil moisture and are not as adversely affected. Plants older than 5 years are probably also not as affected because our data show that they often die out in the center of the grass clump, which forms a shape like a donut ring, which doubles the soil moisture-root interface.

The model predicts that by about year 25 the survival rates for all but the oldest grasses have been adversely affected and there are far fewer perennial grasses on the quadrats.

As mesquite grows to maturity, soil is trapped under the shrub but is not effectively stabilized between individual plants. An irregular surface and a duning effect occurs. This condition often completely eliminates the soil between the plants, exposing any remaining grass roots and the caliche layer. As the duning effect continues, the constant lack of soil moisture and an unstable soil surface amid the dunes eliminates the remaining older plants.

By the 30th year of the simulated period, a community dominated almost solely by mesquite exists. Throughout the simulated period some new plants are established each year as brief favorable growing season conditions permit. These are quickly killed, however, in the harsh microclimate of the interdune area.

RESEARCH NEEDS AND OPPORTUNITIES.—Data for this paper were derived from some 35 quadrats which, plotted over a 30- to 50-year period, yielded almost 7000 observations on black grama plants and some 1600 observations on mesa dropseed. An equivalent number of quadrats remain to be fully processed which would provide a source of information for validating and refining the model, as well as extending it to additional species such as red threeawn (*Aristida longiseta*), tobosa grass (*Hilaria mutica*), and burro grass (*Scleropogon brevifolius*). Data likewise have not been fully processed for some quadrats which were initially mesquite-free (ca. 1915-1925) but now lie lost in the mesquite dunes area. Data from these quadrats would be useful in plotting against Fig. 4. Hopefully, through such analyses, a greater understanding can be gained on the relationship of age structure in stabilizing community development, and further insight can be obtained on the reasons behind the successful invasion of mesquite on Southwestern rangelands.

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Address of authors: R. G. WRIGHT, *Cooperative Park Studies Unit, College of Forestry, Univ. of Idaho, Moscow, ID 83843,* G. M. VAN DYNE, *College of Forestry and Natural Resources, Colorado State Univ., Ft. Collins, CO 80523.*